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Regular research paper

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SPECIES COMPOSITION AND HABITAT CORRELATES OF AMPHIBIAN ROADKILLS IN DIFFERENT LANDSCAPES OF SOUTH-WESTERN POLAND

ABSTRACT: During four seasons (years 2000–2004) on 52.3 km of roads with traffic frequencies ranging from 350 to 10 500 vehicles day⁻¹ and crossing diverse habitats in five regions of south-western Poland 3 742 roadkills from 10 amphibian species were recorded. The most frequent road killed species was common toad *Bufo bufo* (52% of all roadkills), followed by common frog *Rana temporaria* (12%), green toad *Bufo viridis* (11%) and moor frog *Rana arvalis* (3%). For all surveyed roads the roadkill density was positively correlated with the share of woods and the area of ponds. Actual traffic density was a poor predictor of the number of amphibian roadkills in large landscape scale (all surveyed roads). To assess the factors affecting the number of amphibian roadkills in the small landscape scale the Generalized Linear Models (GLZ) were performed between the number of casualties and five habitat variables (area and number of ponds, share of built-up area, open countryside and woodland) for four circular buffer zones (<200 m, <300 m, <400 m, <500 m) around each of the 100-meter sections within 1.8 km of road crossing an area rich in water bodies. The most important variables in GLZ models were the area and number of ponds. These predictors had statistically significant impact on number of roadkills within buffer zones <500 m (area of ponds) and <400 m (number of ponds).

KEY WORDS: amphibian roadkills, amphibian conservation, circular buffers, wildlife road mortality, road ecology

1. INTRODUCTION

Roads and vehicle traffic seriously endanger many amphibian species (Mazerolle 2004), especially those that undertake periodic migration to and from breeding sites (Kuhn 1987, Fahrig *et al.* 1995, Cooke and Sparks 2004, Gibbs and Shriver 2005). The rapid increase of traffic intensity in many parts of Europe, especially on local roads in rural areas (Jaarsma and Willems 2002), may be the main cause for the local amphibian population declines, especially in highly man-transformed landscapes (Fahrig *et al.* 1995, Cooke and Sparks 2004) even if the causes of the global population decrease of this group (Collins and Storfer 2003, Beebee and Griffiths 2005) remain poorly understood (Carrier and Beebee 2003).

At the time of dramatic global amphibian decline recorded currently in many parts of the world (reviews in Collins and Storfer 2003, Beebee and Griffiths 2005) it becomes immensely important to identify and describe the actual levels of losses in

this group of animals. Such studies should be accompanied by the assessment of relationships between large-scale landscape and road parameters and the amphibian mortality level caused by the adverse effect of road traffic (Mazerolle 2004, Orłowski 2007, Puky 2006).

There are many reports of amphibian roadkills but most of them are limited to the species, numbers, and temporal distribution of casualties, and only a few relate number of roadkills to habitat or landscape features (Clevenger *et al.* 2003, Mazerolle 2004, Gibbs and Shriver 2005, Orłowski 2007). A recent study of common toads *Bufo bufo* died on a network of 15 roads crossing an agricultural area of south-western Poland (also covered in this study) demonstrated that the losses in local populations depend primarily on population size and the area of water bodies in the vicinity of roads (Orłowski 2007). That research has also shown that the number of common toads roadkills was not significantly correlated with the traffic volume since their large breeding populations are found exclusively in ponds neighbouring local roads with low traffic volumes (350–470 cars 24 h⁻¹). This results may suggest a long-lasting *cumulative effect* of busy highways leading to decimation or possibly total extinction of local populations (Fahrig *et al.*, 1995, Vos and Chardon 1998, Carr and Fahrig 2001, Mazerolle 2004).

The aim of the present study is to determine the relationships between the habitat structure and the number of amphibian roadkills. We approached this task through large scale comparisons of roads crossing diverse habitats at distant locations as well as through small scale comparisons of single road sections, each conceptually made to a centre of circular buffer zones.

2. STUDY AREAS

We surveyed 52.3 km of 20 roads crossing diverse habitats with different land uses in five regions of Silesia, south-western Poland (Table 1, Fig. 1). The longest (48.8 km) was the network of 15 surveyed roads in the Wrocław Plain. The level of traffic volume was obtained from the data of General Management of Public Roads in Wrocław

and Wrocław District Council for the year 2000 and our own counts performed at all day times. On the majority of surveyed roads the mean circadian traffic intensity ranged from 350 to 470 vehicles day⁻¹ with a major exception of the Wrocław-Opole highway which was by far the busiest with 10 500 vehicles day⁻¹. Environmental characteristics of areas adjacent to roads (number and area of ponds, length of borders with built-up areas, woodlands and agricultural land) were obtained from ordnance survey maps (1:25 000 and 1:10 000) and cadastral data or provided by local authorities.

The Wrocław Plain (*c.* 55 km²) (Fig. 1D) is heavily dominated by arable land (92%) and the share of forests (*c.* 2%) is one of the lowest in Poland. The road in the Bystrzyca Valley, at the outskirts of Wrocław, crosses the area largely covered by deciduous trees including fragments of the natural riverside woodland *Salici-Populetum* (Fig. 1C), with some interspersed of abandoned cropland and eight ponds (0.16–1.0 ha) with lush water vegetation (for more detail see also Ciesiołkiewicz *et al.* 2006). The road in the Stobrawa Forest (Fig 1B) crosses wet deciduous woodland with the predominance of alders *Alnus glutinosa* and birches *Betula verrucosa* and a 0.8 ha pond, about 300 m from the road. The road in Bory Dolnośląskie (widespread forest complex in south-western Poland) runs at the outskirts of village (Chełm Żarski) in the vicinity of a large, 41 ha pond (Fig. 1A). The short (200 m) surveyed section of road in the town of Lubsko (16 000 inhabitants) borders with a small artificial pond (Fig. 1E).

3. MATERIAL AND METHODS

3.1. Roadkill counts

With a partial exception of the Wrocław Plain, the roads were surveyed walking on one side of the road and returning on the other and the roadkills were removed from the road. The road in Bory Dolnośląskie was controlled between 6 a.m. and 7 a.m. three times a week. The road in the Bystrzyca Valley was surveyed between 6 a.m. and 9 a.m. every other day throughout the amphibian migration season (March-May) and 1–2 times

Table 1. The survey areas, duration of field study and characteristics of the 20 road sections in Silesia (south-western Poland), with number of amphibian roadkills in the breeding season (last column). Local geographical names are given in italics, see also Fig. 1. ¹Averages from two consecutive breeding seasons (February–May).

Section	Traffic volume (cars /24 h)	Section length (m)	% built-up area	% open countryside	% woodland	Ponds within 500 m of the road		Total number of roadkills	Roadkills per 1 km / season ¹
						number	area (ha)		
Wrocław Plain: 48.8 km, 24 June 2001 – 18 August 2003									
1.	10 500	3750	67	33	0	2	0.15	6	0.3
2.	5 700	8350	24	76	0	4	0.45	23	0.5
3.	1 900	2400	8	92	0	5	1.12	181	22.5
4.	2 900	2050	73	27	0	3	0.56	25	3.2
5.	2 100	5150	41	59	0	8	1.22	153	10.9
6.	470	2500	60	40	0	4	0.59	46	4.8
7.	350	3450	25	75	0	3	1.25	820	101.7
8.	350	1400	0	100	0	0	0	7	0.7
9.	350	5550	20	80	0	4	0.25	45	1.4
10.	350	3450	25	75	0	4	0.33	19	1.2
11.	350	2850	4	96	0	2	0.07	24	2.3
12.	350	2300	22	78	0	4	0.15	56	10.4
13.	350	2150	28	72	0	3	0.44	14	0.5
14.	350	1050	71	29	0	0	0	2	0
15.	350	2400	10	90	0	1	0.1	18	2.9
Bystrzyca Valley: 0.5 km, 10 March – 24 May 2000 and 2001									
16.	450	500	0	0	100	4	3.345	602	454.0
Bystrzyca Valley: 1.8 km, 1 October 2002 – 30 June 2004									
17.	450	1800	3	53	44.4	9	2.095	465	103.6
Stobrawa Forest: 0.5 km, 1 March – 15 June 2000 and 2001									
18.	400	500	0	0	100	1	0.80	363	294.0
Bory Dolnośląskie: (forest complex): 0.5 km, 9 March – 9 Nov 2001 and 1 February – 15 July 2002									
19.	450	500	0	50	50	1	41	820	639.0
Town of Lubsko: 0.2 km, 1 May – 17 July 2001 and 2002									
20.	400	200	100	100	0	1	0.0025	53	–

a week in other months. The counts on the road in the Stobrawa Forest started at sunrise and took place 3–4 times a week. In the town of Lubsko censuses of casualties were conducted from the beginning of May through to mid July in years 2001 and 2002, respectively. The roads in the Wrocław Plain were surveyed by car at the speed of 20–50 km h⁻¹ and only selected spots (primarily near water

bodies) with abundant roadkills were controlled on foot during the migration season (March–May). All roads were surveyed three times a week between March 15 and September 30, and twice a week in the remaining period. The surveys were conducted on rain-free afternoons and usually took anywhere from 1.5 to more than 3 hours, depending on the weather and roadkill numbers.

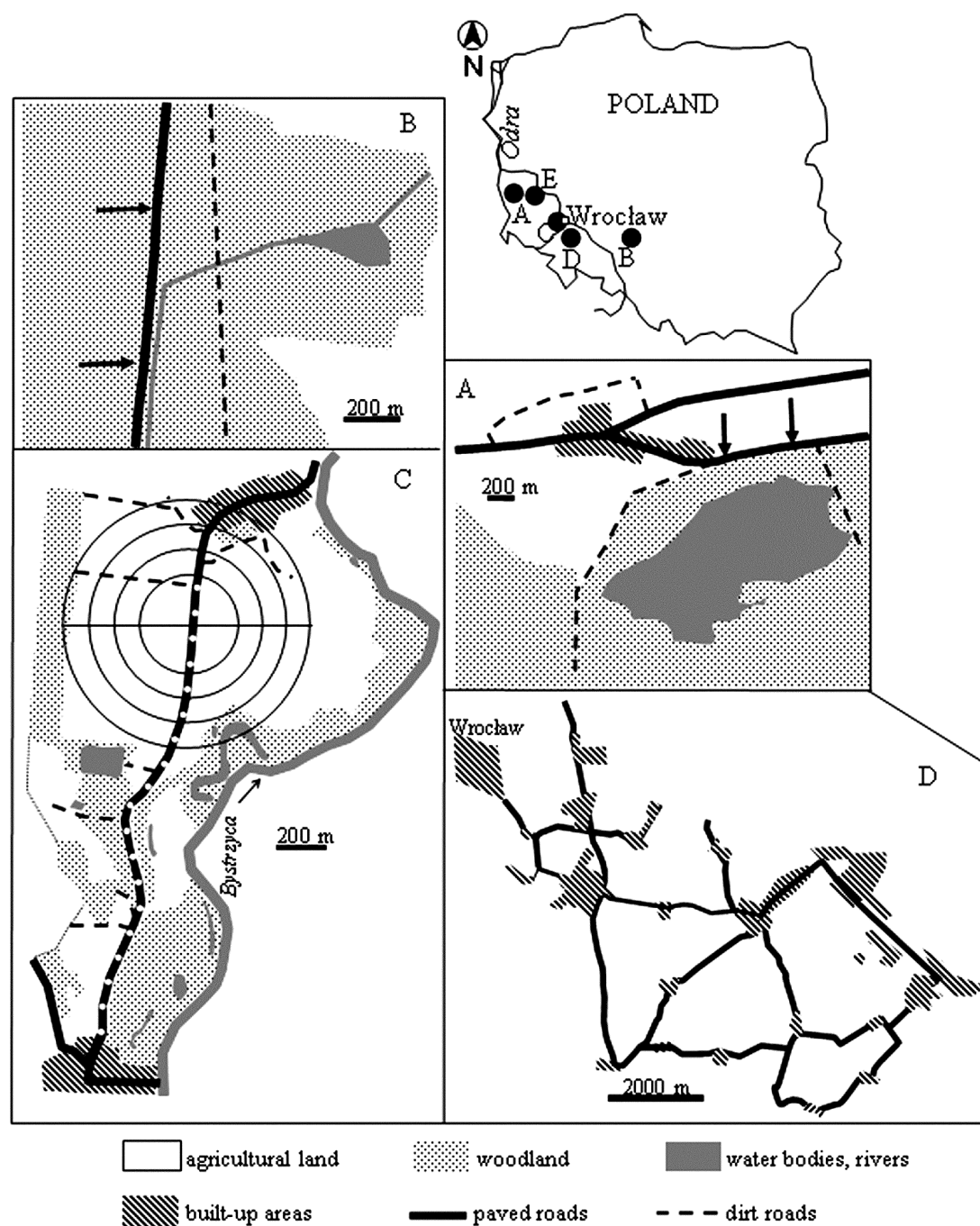


Fig. 1. Roads in Silesia, south-western Poland surveyed for amphibian mortality in the years 2000-2004. A – Bory Dolnośląskie (forest complex), B – Stobrawa forest, C – Bystrzyca Valley, with 18 hundred-meter road sections (separated by white dots) and example of four circular buffer zones (<200 m, <300 m, <400 m, <500 m), D – Wrocław Plain (15 road sections), E – Town of Lubsko (not presented in enlarge). Arrows on Fig. 1A and B indicate the surveyed road section.

3.2. Statistical analysis

Statistical analysis of the collected material was conducted with the help of Statistica 7.0 (StatSoft, 2006) and Excel software. The significance level was 0.05.

Because of the lack of normal distribution (tested in Kolmogorov-Smirnov test) and any possibility of transformation of some road parameters such as traffic volume, we used Spearman rank correlation coefficients (r_s) to calculate the influence of environmental parameters such as the shares of built-up area, open countryside and woodland and the number and area of ponds on the number of roadkills (from March to May, exceptionally in February; no data for this period were available for the road in the town of Lubsko) in all surveyed roads in south-western Poland. The roadkill number on particular sections was calculated per 1 km of road, for which the average value based on two consecutive breeding periods (March-May) was used (compiled in Table 1). The Mann-Whitney test was employed to track the differences in environmental parameters between the surveyed roads.

Spearman rank correlation coefficients, which indicate the direction of a variable's influence, were also used in the framework of the concentric analysis of habitat to calculate the modulatory effect of buffer zones. The concentric analysis of habitat was employed before for the analysis of amphibian habitats (Vos and Chardon 1998, Carr and Fahrig 2001, Pellet *et al.* 2004, Herrmann *et al.* 2005, Rubo and Kiesecker 2005) and mammalian mortality (review in Ramp *et al.* 2005). We defined four circular buffer zones with the radii of <200 m, <300 m, <400 m and <500 m around each of the eighteen 100-meter sections of the 1.8 km stretch of the road in the Bystrzyca Valley (data collected between October 2002 and July 2004). For each buffer zone we determined, with the use of ordnance survey maps (1: 25 000), the relevant habitat parameters, that is, share of built-up area, open countryside, woodland and number and area of water bodies. Since Spearman rank correlation coefficients work only in a univariate analysis, we used the multivariate analysis with a Generalized Linear Model Analysis

(GLZ) (Hosmer and Lemeshow 1989) in software Statistica 7.1 (StatSoft 2006). In GLZ models were applied a Poisson distribution with logarithmic link function (McCullagh and Nelder 1989). To identify the model, the Akaike Information Criterion (AIC) was used to optimise the number and combination of predictive variables included (Burnham and Anderson 2002). To validate the proposed models, the Wald (χ^2) statistics was used to check the significance of the regression coefficient for each parameter. A likelihood ratio test was used to evaluate the statistical significance of including or not including each parameter. Model goodness-of-fit was checked using deviance (Dev.) statistics. Because initial analysis of correlational matrix (Pearson correlation coefficients) between habitat variables had revealed that the variable "number of ponds" was highly correlated with the variable "area of ponds" (Pearson correlation coefficients, $r = 0.86-0.95$) we built two separate GLZ models to introduce the first and then the second of these variables. We assigned the 100-meter road sections to three mortality categories: low with 0–10 casualties ($n = 5$ sections), medium with 10–20 casualties ($n = 7$), and high with 20–80 casualties ($n = 6$) and calculated the differences in environmental parameters between the buffer zones using the Kruskal-Wallis test. Those parameters that had a significant impact on amphibian mortality (obtained in Spearman rank correlation) are shown in Fig. 4.

4. RESULTS

In all five regions of Silesia we recorded the total of 3 742 roadkills from 10 amphibian species (Table 2). The most frequent was common toad *Bufo bufo* which made up two thirds of amphibian roadkills throughout the agricultural Wrocław Plain, followed by common frog *Rana temporaria* and green toad *Bufo viridis* (Table 2).

A distinct majority (88%) of 3 044 amphibian roadkills comes from the breeding season (March-May) and the mortality peaked in the second half of April (Fig. 2). Within the activity season of amphibians their number was lowest (3%) in June and July. A slight increase from the mid August

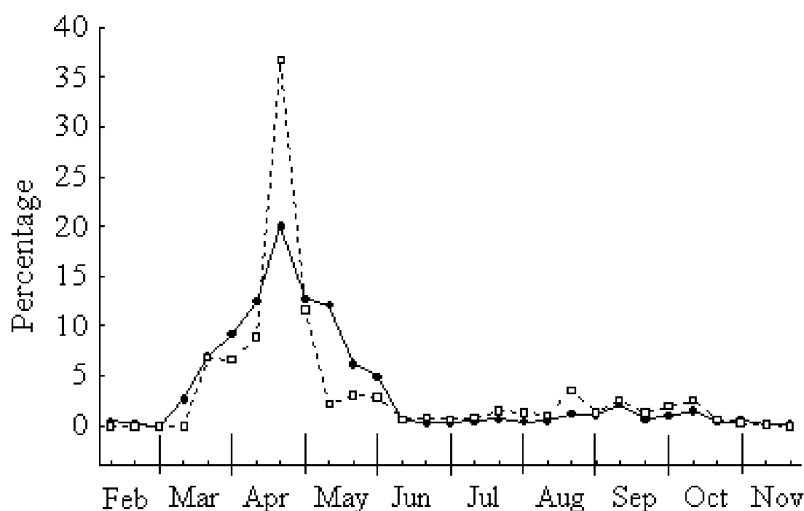


Fig. 2. Dynamics of amphibian road mortality (in % of the total of roadkills) in Silesia in the consecutive 10-day period. Solid line with black dots shows data for all surveyed roads ($n = 3\,742$ casualties), dashed line with white squares shows one full season (2002) data for the road network (48.8 km) of Wrocław Plain ($n = 855$).

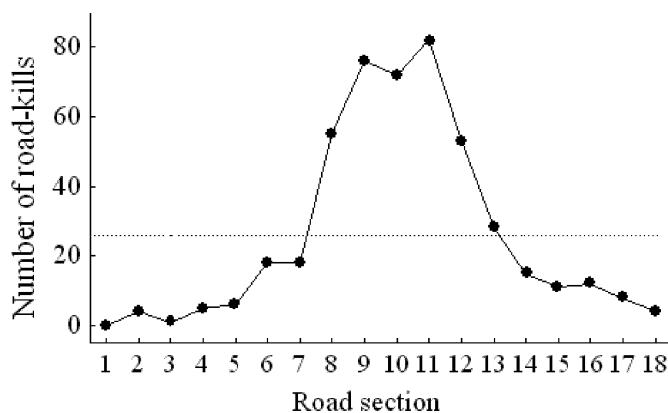


Fig. 3. Number of amphibian roadkills ($n = 465$) recorded on the 18 hundred-meter sections of a local road in Bystrzyca Valley from October 2002 to July 2004 (see Fig 1C). The horizontal dashed line indicates the average (26.0) for the whole study period.

to the beginning of October suggests an autumn migration (Fig. 2).

Out of all relationships describing habitat variation of the studied roads, the highest negative correlation was visible between the share of woodland and built-up areas, while the highest positive one occurred between the pond area and the woodland area (Table 3).

The highest mortality was recorded on roads crossing mosaic forested-agricultural landscapes with water bodies used by amphibians for reproduction, i.e. Bystrzyca Valley, Stobrawa Forest and Bory Dolnośląskie

(Table 1 and 2). The number of amphibian roadkills was positively correlated with the share of woods and pond surface area along the road and negatively correlated with the share of built-up areas (Table 4). This is consistent with the strong positive correlation between the share of woods and pond surface areas as well as the negative correlation between the share of woods and the share of built-up areas (Table 3).

In the agricultural landscape of Wrocław Plain (see Fig. 1D and Table 1) with the pond surface area (within 500 m from road) nearly 27 times (0.44 ± 0.43 ha compared to 11.81

Table 2. Amphibian road-kills in five regions of Silesia, SW Poland. The percentages (%) are given in brackets. See Table 1 for duration of field studies and Fig 1 for location of studies.

Species	Wrocław Plain (48.8 km)	Bystrzyca Valley (0.5 km)	Bystrzyca Valley (1.8 km)	Stobrawa Forest (0.5 km)	Bory Dolnośląskie (0.5 km)	Town Lubsko (0.2 km)	Total of given species
<i>Bufo bufo</i> L.	957 (67)	389 (65)	377 (82)	69 (19)	172 (24)		1964 (53)
<i>Rana temporaria</i> L.	30 (2)	9 (1)	41 (9)	165 (45)	194 (27)		439 (12)
<i>Bufo viridis</i> Laurenti	369 (26)					53 (100)	422 (11)
<i>Rana arvalis</i> Nilsson			1 (<1)		99 (14)		100 (3)
<i>Bufo</i> sp.	69 (5)						69 (2)
<i>Triturus cristatus</i> Laurenti					63 (9)		63 (2)
<i>Pelobates fuscus</i> Laurenti	3 (<1)				54 (7)		57 (1)
<i>Triturus vulgaris</i> L.				19 (5)			19 (<1)
<i>Bombina bombina</i> L.					15 (2)		15 (<1)
<i>Hyla arborea</i> L.			1 (<1)		11 (2)		12 (<1)
<i>Rana esculenta</i> L.	6 (<1)						6 (<1)
<i>Rana</i> sp.	1 (<1)						1 (<1)
Unident. green frogs		98 (16)	6 (1)	10 (3)	97 (14)		211 (6)
Unident. anurans	4 (<1)	106 (18)	39 (8)	100 (28)	11 (1)		364 (10)
Total roadkills	1439	602	465	363	716	53	3742

Table 3. Spearman rank correlation coefficients among the environmental variables reflecting habitat differentiation among the 20 road sections in five localities of Silesia. Asterisks denote significance levels: * – $P < 0.05$, ** – $P < 0.01$.

Variable (see Table 1)	% built-up area	% open countryside	% woodland	Ponds up to 500m		Traffic volume
				area	number	
Length of section	0.28	0.22	–0.57**	–0.03	0.47*	0.11
% built-up area	–	–0.09	–0.65**	–0.32	0.003	0.19
% open countryside	–	–	–0.54*	–0.49*	–0.05	–0.41
% woodland	–	–	–	0.62**	0.004	0.21
Surface area of ponds within 500 m of the road	–	–	–	–	0.54*	0.47*
Number of ponds within 500 m of the road	–	–	–	–	–	0.39

± 19.49 ha; Mann-Whitney test, $U = 3.0$, $P = 0.007$) lower than in other regions (except for the town of Lubsko; see Fig 1A, 1B and 1C), the number of ponds alone turned out to be significantly correlated with the number of roadkills (Table 4).

Our univariate analysis demonstrated that for all four circular buffer zones the number and area of ponds were positively correlated with the number of amphibian roadkills (Fig. 3) (Table 5). The negative impact of built-up areas resulted from the local

landscape features, especially from the location of water bodies far from settlements. Built-up areas occurred mainly around road sections with small roadkill number (Fig. 4). The number and area of ponds increased clearly in consecutive buffer zones and was highest around the sections with high roadkill number (Fig. 4).

Our multivariate analysis revealed that results of GLZ were similar for the model with the variable “area of ponds” and “number of ponds”, although the impact of par-

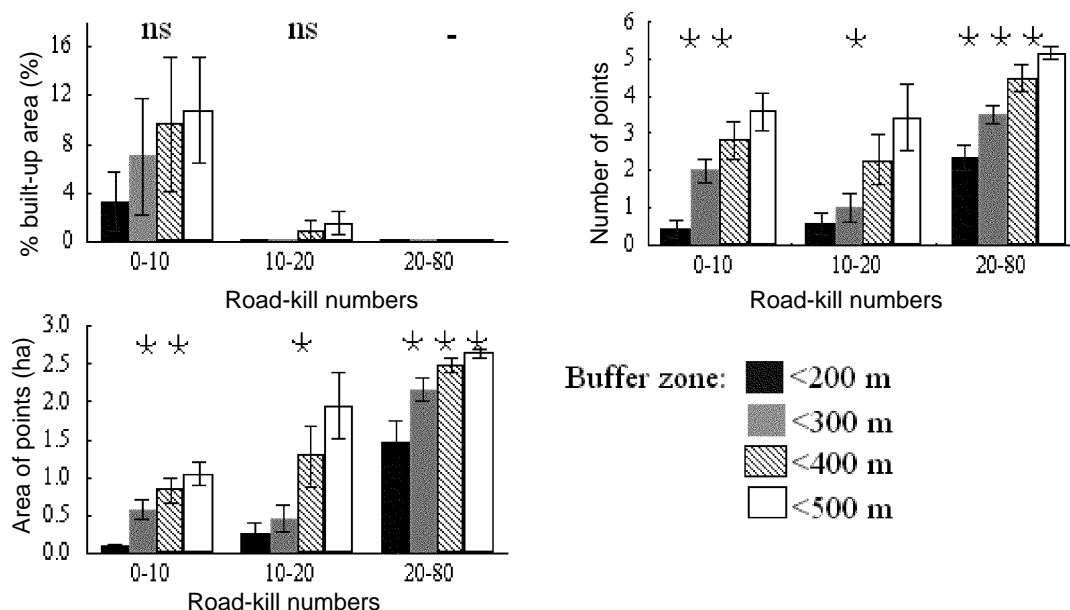


Fig. 4. Comparison of the average (\pm SE) habitat parameters within four concentric buffers embracing 18 hundred-meter road sections with three ranges of roadkill numbers in Bystrzyca Valley (1.8 km), Oct 2002 – Jul 2004 (see Fig. 1C and Table 5). Ranges of roadkill numbers calculated for five (range: 0–10 roadkills), seven (10–20) and six (20–80) road sections. Charts show the differences between the comparable parameters in four specified circular buffers obtained in Kruskal-Wallis test (for all cases with three degrees of freedom); Asterisks denote significance levels: * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$; ns – not significant ($P > 0.05$).

ticular variables varied in consecutive buffer zones (Table 6). In both models the highest values of the parameter estimates (Wald- χ^2) were obtained in the second buffer zone (<300 m). In general, the “area of ponds” had more effect on the number of roadkills than the “number of ponds”, especially in the case of fourth buffer zone (<500 m), in which only the first mentioned variable was statistically significant. In the model with the variable “area of ponds” the key importance for the number of roadkills (= statistically significant in each buffer zone) was related to two variables: “area of ponds” and “% open countryside”. In the second model variable “% open countryside” was statistically significant in two buffer zones (<300 m and <500 m). The variable “share of woodland” had statistically significant effect only within the first buffer (<200 m) in two constructed models.

5. DISCUSSION

In Silesia, like in many other parts of Poland and Europe the most often road-killed species was common toad (e.g. Fuellhaas

et al. 1989, Hels and Buchwald 2001, Baldy 2002, Rybacki 2002, Cook and Sparks 2004, this study). High mortality of this species is connected mainly with: 1) high density in terrestrial (also in man-dominated) habitats, 2) long-distance (up to 2 km) migration during breeding season, 3) very slow speed of moving and often pair formation (*in amplexus*) during migration, 4) philopatry to the breeding sites, which may also act as ecological trap in the case of building a new road (Heusser 1968, Sinsch 1988, Hels and Buchwald 2001, Schlaepfer *et al.* 2002, Cook and Sparks 2004, Orłowski 2007). The second species of the toad (green toad) was recorded only on the road sections located in (or near) built-up areas (Wrocław Plain and Town Lubsko, see Table 2). Our results may confirm earlier studies, which indicates that villages are the main habitat inhabited by the green toad within agricultural areas of western Poland (Rybacki and Berger 1997). The third most often killed species, common frog dominated in mosaic landscapes fragmented by woodland and agricultural areas (Bory Dolnośląskie and Sto-

Table 4. Spearman rank correlation coefficients (r_s) between amphibian roadkill density and environmental variables of roads in Silesia. Asterisks denote significance levels: * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$.

Variable	Length of sec- tion	Traffic volume	% built- up area	% open country- side	% wood- land	Ponds within 500 m of the road	
						area	number
<u>All localities except for the Town Lubsko (19 roads , 52.1 km)</u>							
Roadkills per 100 m in the breed- ing season, Feb-May (<i>n</i> = 3 120) ¹	-0.40	0.18	-0.56*	-0.25	0.70**	0.81***	0.29
<u>Wrocław Plain (15 roads, 48.8 km)</u>							
Roadkills per 100 m in the breed- ing period, Feb-May (<i>n</i> = 1 075) ¹	0.12	0.02	-0.21	0.19	–	0.65**	0.54*
Total of roadkills (<i>n</i> = 1 439)	0.33	0.10	-0.16	0.14	–	0.75***	0.73***

¹ See Table 1

Table 5. Spearman rank correlation coefficients (r_s) between the number of amphibian roadkills ($n = 465$) on one hand and habitat variables in each of the four circular buffers (<200 m, <300 m, <400 m, <500 m) around 100-meter road sections in the Bystrzyca Valley on the other. Asterisks denote significance levels: * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$.

Variable (average; min-max) ¹	Spearman rank correlation (r_s)			
	<200 m	<300 m	<400 m	<500 m
%built-up area (2; 0–30)	-0.50*	-0.63**	-0.81***	-0.89***
%open countryside (57; 0–98)	0.39	0.37	0.12	0.10
%woodland (28; 0–65)	0.06	-0.30	0.18	0.04
Number of ponds (3; 0–7)	0.74***	0.69**	0.74***	0.70**
Area of ponds [ha] (1; 0–3)	0.81***	0.77***	0.81***	0.84***

¹Extreme and average values of variables compiled for 72 data points (= 4 circular buffer zones × 18 road sections).

brawa Forest, see Table 1 and Fig. 1). It also confirms the heavy relation of the common frog with both this habitats, although this species is considerably less abundant within simplified agricultural landscapes (Johansson *et al.* 2005).

The striking domination of both toad species (96% of all victims), among the road-killed amphibians in Wrocław Plain may indicate a rather small habitat diversity, especially the scarcity of water bodies and the virtual lack of forests within the study area. The highest amphibian diversity, including some scarce species (*Rana arvalis*, *Hyla arborea*, *Triturus cristatus*, *T. vulgaris*, *Bombina*

bombina; Table 2) was recorded in areas with a wide spectrum of habitats, rich in ponds and woodlands (see Table 1, Fig. 1).

The factors shaping the large-scale amphibian mortality (on all surveyed roads in south-western Poland) included the share of woodland border and pond surface area (both positive) and share of built-up areas (negative). These relationships result from the fact that the most abundant breeding amphibian populations considered here (Bory Dolnośląskie, Stobrawa Forest, Bystrzyca Valley) were concentrated in big water bodies situated within woodland outside human settlements. However, the non-random

Table 6. Results of generalized linear models (GLZ) with Poisson distribution and log-link function of the habitat variables affecting the amphibian roadkill numbers along eighteen 100-meter sections of road in the Bystrzyca Valley within four circular buffers (<200 m, <300 m, <400 m, <500 m). ¹ As exponential of parameter estimates the Wald- χ^2 are given.

Effect	Exponential of parameter estimates ¹			
	<200 m	<300 m	<400 m	<500 m
<i>MODEL WITH THE VARIABLE "area of ponds"</i>				
%built-up area (%)	0.413	0.420	1.033	0.239
%woodland (%)	8.646**	0.028	1.762	2.070
%open countryside (%)	7.306**	18.169***	9.435**	10.606**
Area of ponds (ha)	9.841**	24.901***	10.378**	5.208*
<i>Goodness-of-fit of whole model</i> ²	15.208	8.707	13.486	13.222
<i>MODEL WITH THE VARIABLE "number of ponds"</i>				
%built-up area (%)	0.465	0.390	0.577	1.694
%woodland (%)	9.993**	0.127	0.011	1.381
%open countryside (%)	1.945	11.534***	3.277	6.650**
Number of ponds	9.278**	31.106***	9.883**	0.735
<i>Goodness-of-fit of whole model</i> ²	13.863	7.463	13.092	17.672

¹ Extreme and average values of variables compiled for 72 data points (= 4 circular buffer zones \times 18 road sections).

² Model dispersion factors are given by deviance (Dev.). Asterisks denote significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

selection of study plots may prove to be the major drawback of this study, especially with regard to mortality assessment on short road sections adjoining large amphibian breeding sites (with the exception of roads in Wrocław Plain, where surveys were conducted on the whole road network, see Table 1). It must be remembered that the amphibian road mortality is known to occur mostly in local roadkill hotspots (Rybacki 1995, Clevenger *et al.* 2003, Cooke and Sparks 2004), which places a caveat on extrapolations to large areas. The comparison of the relationships between habitat parameters and amphibian mortality level, both on all surveyed roads in south-western Poland as well as on the road network in Wrocław Plain showed however, that only the variable "area of ponds" had a statistically significant effect on the victim number in both these data sets (Table 4). In fact, except for the Wrocław Plain, the roads surveyed in this study were deliberately selected to cross amphibian-rich habitats, and, in addition, the pond area was positively correlated with traffic volume (see Table 3) hence our results for all roads in south-western Poland presented in Table 4 may be skewed towards high local number of roadkills.

The decisive impact of water bodies on the number of amphibian roadkills was also evident with the consideration of much more accurate concentric analysis of biotopes in Bystrzyca Valley (Tables 5 and 6). Statistically significant influence of the number of water bodies on the number of casualties was recorded within 400 m either side of the road, and the area of water bodies affecting the number of roadkills within 500 m (Table 6). Despite the large extent of migration of both victim species, which in common toad can reach up to 2200 m and in common frog up to 800 m (Blab 1986), GLZ models obtained in this study (see Table 6) may point to the critical importance of number of ponds situated within 400 m of roads in shaping of these species' level of number of casualties. These results can have practical implications in spatial planning and designation of protection zones around water bodies at the time of modernization or construction of new roads. It seems necessary to exclude a zone of at least 300–400 m around the pond. The buffer zone protection is practiced mainly in the United States; however the legally approved extent of such zones, below 35 m, is much smaller

there (discussed in Herrmann *et al.* 2005). It must be stressed, however, that based on the results of research of road traffic impact on amphibian populations (see references below) the width of the protective zone should also depend on the amphibian species composition. According to Semlitsch (1998) the more sedentary urodels, rarely migrating beyond 200 m from breeding sites will require smaller buffer zones. It must be also remembered that the extent of the buffer zones is directly reflected in the survival rates of the amphibian populations. For example the median road mortality rate for spotted salamander *Ambystoma maculatum* was c. 17% for individuals moving annually 100 m, and 37% for those moving 500 m (Gibbs and Shriver 2005).

The buffer zone-based research carried out so far has proved that the spatial impact of roads and road traffic on the abundance of breeding amphibian populations may be much more pronounced. According to Forman (2000) the general road-effect zone comprises from 200 to 800 m, which is partly consistent with the results of our study, especially for the model with the variable “area of ponds”, which was statistically significant within radius of <500 m (Table 6). Vos and Chardon (1998) proved that the most adverse effect of roads on the moor frog *Rana arvalis* population (migratory species, as common toad and common frog) was within the radius of 250 m around the breeding pond, although it was still visible up to 750 m. Carr and Fahrig (2001) showed the negative road impact on the abundance of *Rana clamitans* within 1.5 km, which reflects the extent of migration in this species. In the European tree frog *Hyla arborea* impact of vehicular traffic was greatest up to 400 m from the breeding pond, although the negative influence of built-up areas was detected as far as 1110 m away (Pellet *et al.* 2004).

Our analysis confirms that traffic density is a poor predictor of the number of amphibian roadkills (Table 3), which has been interpreted as a *cumulative effect* of the decimation and extermination of amphibian populations near busy highways (Fahrig *et al.* 1995, Vos and Chardon 1998, Carr and Fahrig 2001, Mazerolle 2004). It must be stressed,

however, that on a single road section traffic density will be the main factor shaping the mortality level of amphibians (Gibbs and Shriver 2005), with the critical importance of night-time traffic, which coincides with the peak of activity in some species (Hels and Buchwald 2001, Mazerolle 2004).

The methods used in this study could possibly also be blamed for the underrepresentation of some taxons. In Wrocław Plain counts were made using a car and in relatively long intervals (2–4 days), which might contribute to the lower detectability of thin-skinned species such as newts *Triturus* sp. and frogs, easily destroyed and disappearing from the road surface (in details described in Hels and Buchwald 2001). Although on the other hand, *H. arborea* was not recorded as breeding species and newts (both species) and *Pelobates fuscus* are very rare in Wrocław Plain and their presence was detected only in five and two ponds located near the surveyed roads (G. Orłowski – unpubl.). In the rest areas surveyed in Silesia the counts of roadkills was made by foot, which may favoured the detectability of small and thin-skinned amphibians.

The ominous absence of amphibians in water bodies adjacent to busy highways (Vos and Chardon 1998, Carr and Fahrig 2001, Gibbs and Shriver 2005) combined with the alarming general decrease of their populations (Carrier and Beebee 2003, Cooke and Sparks 2004) and the rapid expansion of roads in central and eastern Europe are good reasons for concerns about the future of European amphibians and for demanding a better control of road planning and building.

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